Growth and Mortality in the Ribbed Mussel *Geukensia demissa*

(Bivalvia : Mytilidae)

BY

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(5 Text figures)

INTRODUCTION

ON THE EAST COAST of North America *Geukensia* (formerly *Modiolus* and *Arcuatula) demissa* (Dillwyn, 1817), is a major component of salt marsh communities. This mud-dwelling mussel is generally found in close association with the salt-tolerant angiosperm *Spartina alterniflora* and occurs from the Gulf of St. Lawrence, to northeast Florida (ABBOTT, 1974). *Geukensia demissa* is highly eurytopic, being able to tolerate temperatures of —22° C to 40° C (KANWISHER, 1955; LENT, 1969) and salinities of 5‰ to 75‰ (WELLS, 1961; LENT, 1969). This tolerance for environmental extremes allows *G. demissa* to inhabit an extremely high intertidal habitat, where it is exposed to terrestrial conditions for up to 83% of the time (KUENZLer, 1961).

The present study was stimulated by the observation that mussels found on the outer coast of Maryland were noticeably larger than conspecifics which penetrate a considerable distance into the Chesapeake Bay estuary. It was hypothesized that this situation could arise from three documented patterns: 1) The growth rates and maximum attainable sizes of the mussels could vary between habitats due to differences in the physical environment as found in other marine organisms (SEED, 1969; LEWIS & BOWMAN, 1975; PAINE, 1976). Environmental variation could cause this pattern either by direct physiological limitations on growth rates in a particular physical regime or by causing parallel variation in critical resource levels. 2) Predation pressure could be less severe in the outer coast environment so that the larger outer coast mussels could be attaining a size refuge from predation (as in CONNELL, 1972). 3) Growth rates and survival could be density dependent, enabling sparse mussels to reach larger sizes (as in SUTHERLAND, 1970).

This paper presents data on the population structure, growth rates, predation intensity, and mortality of mussels from three locations along the Chesapeake Bay to elucidate the cause of this size pattern. Since intraspecific variation in the size attained by bivalves in different habitats can be accompanied by divergence in shell shape (SEED, 1968), consideration is also given to the allometric relationships of the mussels at the three study sites.

METHODS

Study Sites

Three study areas were selected to represent differences in salinity and temperature fluctuation on a gradient from the open coast to well within Chesapeake Bay (Figure 1). The most conspicuous biotic component of all three study sites was the grass *Spartina alterniflora*, on whose roots *Geukensia demissa* is predominantly found. The Tom's Cove study site on Chincoteague Island (37°52′N, 75°25′W) is an extensive lagoonal salt marsh. The fauna and flora of this area are similar to those described by TEAL (1962). The second study area, Cape Charles (37°10′ N, 76°00′W), is located on the inside mouth of Chesapeake Bay. The third sampling location, Crisfield (37°25′ N, 76°00′W), is located well into Chesapeake Bay. The areas sampled at the last two sites, within Chesapeake Bay proper, were the small fringe marshes characteristic of these areas.

Annual temperature and salinity fluctuations in the Chesapeake Bay area are extremely great. At Crisfield, for example, water temperatures range from 0° C to 32° C, while salinities range from 13.7‰ to 20.4‰ annually (1959-1961). From Chesapeake Bay to the outer coast

On page 62 of our July 1980 issue there appears a very serious error. We are totally mystified as to how it did occur since the wrong line was neither in the manuscript nor in the galley proofs submitted to and returned by the author. Unfortunately, the same error was also introduced on the index page. We present herewith a corrected substitute page with the request that it be inserted in place of the offending page and that the word Dreissenacea be stricken out on the index page. We assume full responsibility and offer our apologies to our readers, but especially to the author.   R. Stohler, Editor
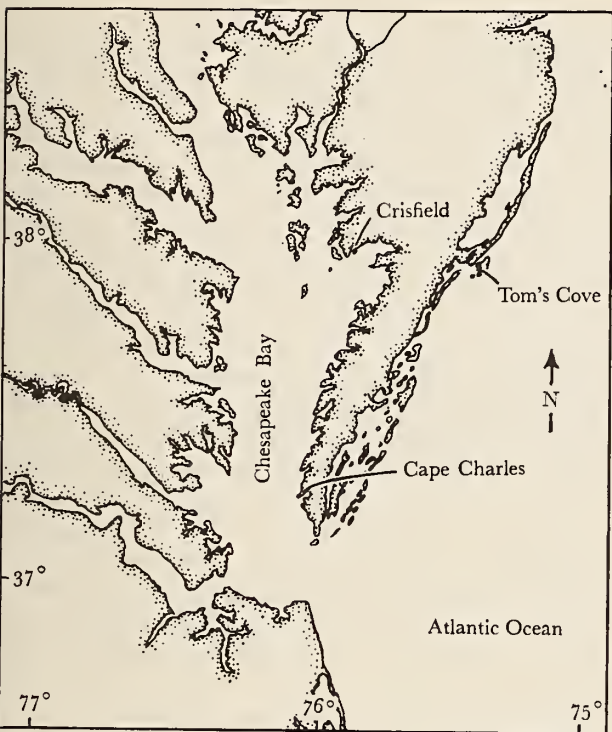
Figure 1

Map of the Chesapeake Bay Area showing the Study Sites

these extremes are considerably reduced due to the buffer-ing effect of the Atlantic Ocean. Annual monthly mean temperatures and salinities for the three study areas re-flect this trend, even though the extremes are masked. At Crisfield mean monthly conditions have a range of 2.6° C to 28.1° C and 15.3‰ to 17.8‰. At Cape Charles, which is located at the mouth of Chesapeake Bay, mean monthly conditions range from 4.6° C to 26.3° C and 20.1‰ to 24.3‰. Outside of Chesapeake Bay at Wachapreague, Virginia mean monthly water conditions range from 4.6° C to 26.2° C and 27.5‰ to 32.8‰. These data are from government records (U.S.D.C., 1973), except for the open coast site (Wachapreague, Virginia) which were provided by the Virginia Marine Institute. The Wacha-preague data are for a location similar to the Tom's Cove study site and are thought to accurately represent the physical environment at Tom's Cove. These data illustrate the differing environmental conditions at which organ-isms at the study sites are exposed while submerged, and indicate a gradient of increasing physical stress from the open coast into Chesapeake Bay. Terrestrial environmen-tal conditions would also be expected to exhibit this pat-tern due to the buffering effect of the open ocean on local climate.

Sampling Methods and Measurements

At each site at +0.5 m above mean tidal height a $\frac{1}{4}$ m^2 quadrat was tossed randomly into thick *Spartina alterni-flora* cover harboring *Geukensia demissa*. This was re-peated 5 times at each study site. To supplement this sampling, at each site 5 additional quadrats were hap-hazardly tossed into areas of identical tidal height, but without dense *S. alterniflora* cover. Each study site was also intensively searched for empty shells and the shells were examined for signs of predation. All sampling was done in November 1976.

In the laboratory the collected mussel clumps were sep-arated and sieved to retain all mussels larger than 2 mm, a process that should assure detection of most newly settled mussels (LOOSANOFF & DAVIS, 1953). Mussels were then cleaned of epiphytes and byssal threads, aged, and meas-ured.

Mussels were aged by counting external growth rings (annuli) on the shells. Growth rings are caused by retrac-tion of the shell-secreting mantle edge into the shell dur-ing harsh environmental conditions. The degree of devel-opment of these rings, therefore, will be proportional to the stress that caused them (SEED, 1969). In the Chesa-peake Bay area both temperature and salinity are highly variable seasonally resulting in the formation of strong annual rings. Disturbance rings caused by other than sea-sonal events are relatively minor and easily distinguished from major seasonal interruptions. Lent (personal com-munication) has verified that the disturbance lines in Del-aware Bay *Geukensia demissa* represent annual lines. The method used to count the growth lines was identical to that described by SEED (*op. cit.*). First year growth was considered to be the first annual growth ring found after the spat settled.

After aging, each mussel was measured to 0.01 mm with vernier calipers for length (maximum anterior-posterior dimension), height (maximum dorso-ventral dimension), and width (maximum lateral axis dimension). Then each mussel was opened and its tissue removed. Both the shell and tissue were dried at 75° C to a constant dry weight and weighed to 1 milligram on an analytical balance.

RESULTS

Population Structure

Quadrat sampling indicated that mussel densities were considerably higher at Tom's Cove than at the other two more estuarine study areas. A total of 528 *Geukensia demissa* were collected at Tom's Cove (140, 70, 108, 115, and 95 mussels found in individual quadrats, $\overline{X}$ *G. demissa* per $\frac{1}{4}$ m² = 105.6). At Cape Charles 5 quadrat samples yielded a total of 111 mussels (33, 39, 18, 12, and 9; $\overline{X}$

G. demissa per $\frac{1}{4}$ m² = 22.2). At Crisfield 5 quadrats yielded 65, 45, 22, 40, and 61 mussels ($\overline{X}$ *G. demissa* per $\frac{1}{4}$ m² = 46.6) for a total of 233. Quadrat sampling on substrate lacking *Spartina alterniflora* at Tom's Cove revealed densities of 12, 8, 0, 4, and 18 *G. demissa*, while at the other 2 locations mussels were only found closely associated with *S. alterniflora*. These two patterns where (1) *G. demissa* densities decrease from the open coast to more estuarine environments, and (2) high *G. demissa* densities are found associated with the marsh grass *S. alterniflora* agree with all my observations in the Chesapeake Bay Area.

Figure 2 illustrates the size (length) distribution of mussels found at each study site. There is a progressive increase in both the average and maximum size of the mussels from Crisfield to Cape Charles to Tom's Cove. This is correlated with their position along the temperature/salinity gradient. Both the Tom's Cove and Crisfield populations approximate a normal distribution of body sizes; however, the Cape Charles population is distinctly bimodal.

The age distributions of the 3 mussel populations are illustrated in Figure 3. In the Tom's Cove population
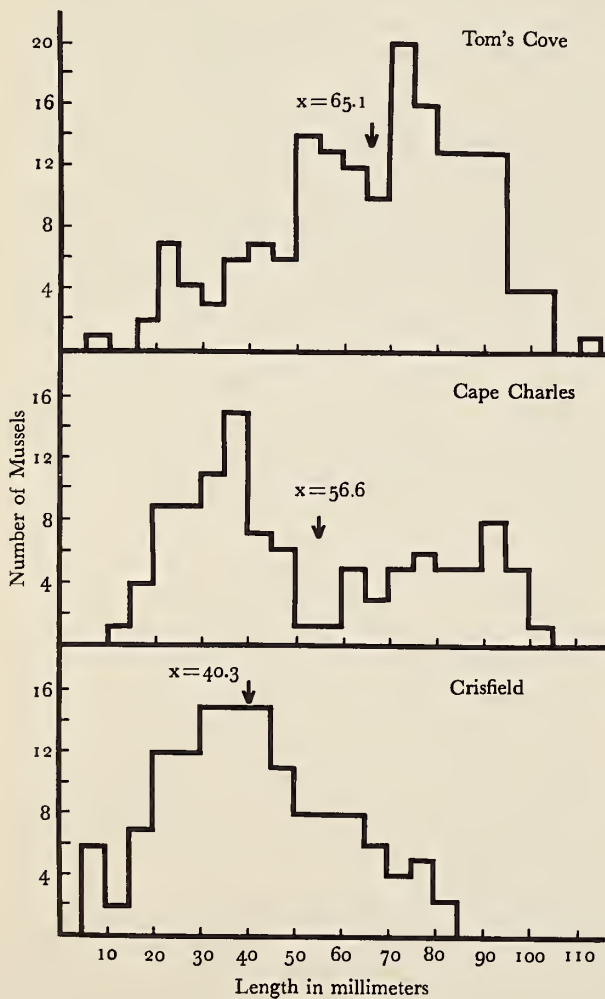
Figure 2

Shell lengths histograms of the *Geukensia demissa* individuals sampled at the three study sites (Tom's Cove, n=210; Cape Charles, n=111; Crisfield, n=133)
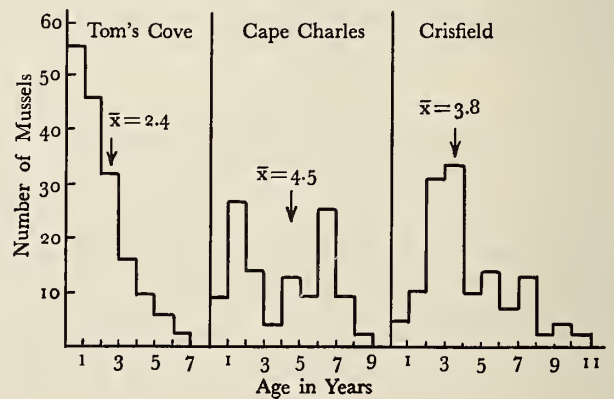
Figure 3

Age histograms of the *Geukensia demissa* individuals sampled at the three study areas (Tom's Cove, n=210; Cape Charles, n=111; Crisfield, n=133)

there is a constant attenuation of the number of individuals with increasing age, implying predictable recruitment and constant mortality. In the Cape Charles and Crisfield populations age class representation is erratic, indicating unpredictable settlement or survival of juveniles. The bimodal nature of the Cape Charles size class distribution is also evident in the age class structure (Figure 3).

The break in the age class distributions corresponds to a lack of four-year-old mussels. Four years before the samples were taken a severe tropical storm hit the Chesapeake area (Tropical Storm Agnes, July 1972). The storm was followed by lowered salinity in much of the bay, which was known to have had a detrimental effect on the marine epifauna (ANDREWS, 1973). Data from the present study indicate that *G. demissa* population recruitment was hampered by the storm, either by reduced fecundity of adults or high mortality of mussel larvae and recently settled juveniles.

The age distribution of the 3 populations shows a progressive increase in the longevity of *Geukensia demissa* from the outer coast study site to the estuarine Crisfield location. This increase is contrasted by the decrease in mussel size observed along the same gradient.

Growth Rates

Cumulative growth curves for the mussels sampled at each study site, constructed by averaging the sizes of individuals found in each age class, are presented in Figure 4. At each location the mussels have an attenuating growth rate with age. The growth rates differ significantly between sites ($p < 0.05$, ANOVA). Growth rates are highest on the outer coast (Tom's Cove) and decrease as one moves into Chesapeake Bay (Cape Charles and Crisfield).
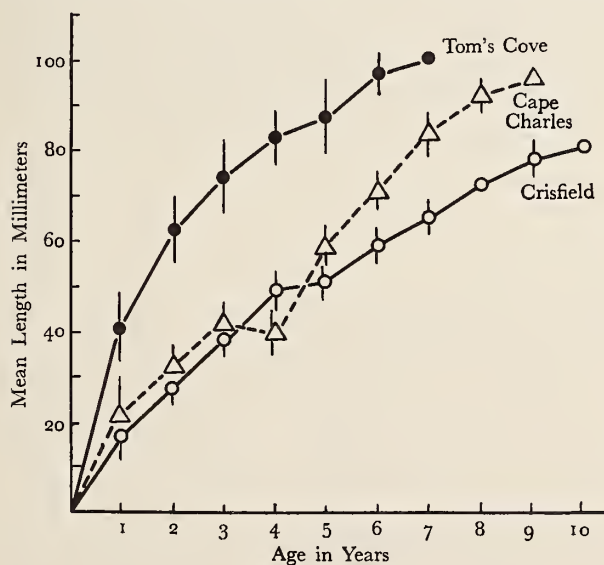

Figure 4

Cumulative growth curves for the *Geukensia demissa* found at the three study sites. Vertical bars indicate one standard deviation and accurately reflect statistical differences (< 0.05, ANOVA)

The differing maximum and average size of mussels from the 3 study sites (Figure 2), then, appear to be attributed to growth rate differences.

The four-year-old Cape Charles mussels show a reduced growth rate which is anomalous relative to the other age classes (Figure 4). This again points to the effect of the tropical storm that year.

Mortality

As has been noted by previous researchers (LENT, 1969; KUENZLER, 1961) predation on *Geukensia demissa* does not appear to be common. This probably results from the higher intertidal position of *G. demissa,* which is physiologically too stressful for most potential marine predators. CONNELL (1970) has suggested that in physically stressful environments predation is rarely sufficiently potent to alleviate competition among prey species. However, in the extremely high intertidal salt marsh environment, *G. demissa* has no apparent interspecific competitors.

At each study site thorough searches were made for loose, empty *Geukensia demissa* shells to assess the cause of their death. Approximately equal areas were searched at each location. A total of 92 empty whole shells were found (55 Tom's Cove, 21 Cape Charles, and 16 Crisfield) and carefully examined for evidence of predation. Shells varied greatly in condition, indicating that they remained in the vicinity of their death for considerable periods of time. None of the mussels, however, gave any evidence of mortality due to predation.

Potential predators of *Geukensia demissa* at the study sites included gastropods, birds, crustaceans, a ray, and terrestrial mammals. Most of these predators damage the shells of bivalve prey and their presence would be detected by examining dead shells. None of the gastropod predators observed at the study sites (*Busycon canaliculatum, Urosalpinx cinereus, Eupleura caudata,* and *Polinices duplicata*) were observed as high as the *Spartina alterniflora/ Geukensia demissa* association on the beach. The latter 3 gastropod species are drills and would leave distinctive drill holes (CARRIKER, 1955). Bird predation would also leave damaged shells as evidence of their activity (NORTON-GRIFFITHS, 1967). The blue crab *Callinectes sapidus* was found at all 3 study areas high enough on the beach to prey upon *G. demissa*. However, the crab's access to the mussels could be severely hampered by *S. alterniflora,* and its feeding method would involve shell damage which could be detected in the field. The cow-nosed ray, *Rhinoptera bonasus,* is an important local molluscivore, but confines its activities to deeper waters than those inhabited by *G. demissa* (R. Orth, personal communication). KUENZLER

(1961) suggests that the raccoon, *Procyon lotor,* is an important predator on ribbed mussels. Emerged *G. demissa* respond quickly to shadows or disturbance by closing their valves, a response which is conveyed to other mussels within a clump (LENT, 1969) and strongly suggests adaptation to resist terrestrial predators. The strong byssal thread attachment of *G. demissa* would also deter predation by mammals. At some locations, predation by *P. lotor* is evident by animal tracks and broken shells (S. K. Pierce, personal communication). However, predation by *P. lotor* appears to be localized and was not observed at any of the study sites.

Predation, however, could limit the lower vertical distribution of the mussels, since the majority of their predators are found in the lower intertidal zone. S. K. Pierce (personal communication) found that *in situ Geukensia demissa* experienced little or no predation at his study area (Alligator Point, Florida), but mussels transferred to the adjacent subtidal zone experienced severe predation within a week by a gastropod drill.

Since predation does not appear to be an important factor in mussel mortality, the cause of *Geukensia demissa* death is of interest. Most empty shells were found still attached by their byssal threads within thriving clumps of mussels, and not collected on the searches for loose mussels. Dead *in situ* mussels were observed at Tom's Cove and Crisfield, but none could be found at Cape Charles. The quadrat sampling confirmed this observation. At Tom's Cove 35 dead *in situ* mussels were collected representing 16.6% of the quadrat mussels ($\overline{X}$ density = 105 per $\frac{1}{4}$ m^2). Thirteen dead *in situ* *G. demissa* were found (12% of total) at Crisfield ($\overline{X}$ density = 46.0 per $\frac{1}{4}$ m^2). At Cape Charles mussel density was low ($\overline{X}$ = 22.2 per $\frac{1}{4}$ m^2) and no dead *in situ* mussels were found. These results suggest that the occurrence of dead *in situ* mussels is density dependent. Density dependent mortality implies that intraspecific competition may be a significant mortality factor in *G. demissa* populations.

Figure 5 shows size and age histograms for the *in situ* dead mussels from Tom's Cove. In contrast to comparable histograms for the live populations (Figures 2, 3), these distributions from Tom's Cove reveal that the dead mussels were significantly older (p < 0.05, ANOVA) but were not larger (p > 0.05, ANOVA) than the living mussels. This is probably due to the fact that small mussels are capable of considerable movement, while large mussels are incapable of mobility due to their bulk. The length at which mussels become virtually sessile has been shown to be approximately 45 mm (LENT, 1969). This corresponds with the increased incidence of dead *in situ* mussels found

Figure 5

Size and age histograms of the dead *in situ Geukensia demissa* found in the Tom's Cove quadrats

in the mussel clumps (Figure 5). Small mussels apparently are able to avoid density-dependent mortality by their mobility, but as they become immobile with increased size they become vulnerable to density-dependent mortality. Similarly, HARGER (1968, 1972) showed that the small mussel, *Mytilus edulis,* by virtue of its mobility, competitively excludes the large *M. californianus* in protected waters. This is accomplished by moving to the outside of mussel clumps and avoiding competition for space resulting in the death of the large *M. californianus.*

The mechanism whereby immobile *Geukensia demissa* suffer density-dependent mortality, however, is not clear. (1) Disease and parasites are potentially density-dependent mortality factors, but no data are available to clarify this possibility. (2) The larger mussels could be crushed in the growing clump. However, the fact that larger heavier shells of the mussels were found dead *in situ,* and the fact that none had damaged shells argue against this possibility. (3) A large immobile mussel could be trapped in a position where it encounters siltation that could impede both feeding and respiration. Reduced growth rates and size of dead mussels support this conclusion. Comparison of the shell size parameters of the two most common age classes of dead *in situ* mussels with the comparable age classes of live mussels from Tom's Cove (Table 1) reveals that dead mussels in these age classes were significantly smaller than living mussels (p = 0.05, ANOVA).

Table 1

Mean Sizes (millimeters ± standard deviation) of 3- and 4- year old *Geukensia demissa*
found either dead or alive in Tom's Cove mussel clumps.

	3 years old				4 years old			
	N	$\overline{X}$ Length	$\overline{X}$ Width	$\overline{X}$ Height	N	$\overline{X}$ Length	$\overline{X}$ Width	$\overline{X}$ Height
Dead Mussels	10	64.6 ± 8.0	27.1 ± 2.9	20.0 ± 2.2	10	74.8 ± 7.5	31.5 ± 3.7	23.3 ± 2.9
Alive Mussels	32	78.7 ± 7.8	32.8 ± 2.6	24.0 ± 2.1	18	88.1 ± 7.1	34.4 ± 2.0	27.4 ± 1.5

All size differences between dead and alive mussels are significant at the $p < 0.05$ level (ANOVA).

Shell Shape and Size

Since shell allometry can be modified in mussels by growth rate and density (SEED, 1968), shell growth was investigated in the populations studied. Regressions of shell height and width upon shell length (Table 2) were highly significant at each study area. However, these relationships did not differ significantly between study areas ($p > 0.05$, ANOVA). In *Mytilus edulis* both high density and increased growth rates caused mussels to grow more rapidly in length than in the other dimensions (SEED, 1968). If this were the case in the present study, mussels from Tom's Cove with higher population densities and growth rates would have indicated this trend. In addition, SEED (*op. cit.*) found that as *M. edulis* grows in length, the height to width ratio decreases significantly. This was found to be

the case with the *Geukensia demissa* in this study (Table 2). However, the relationship was not altered significantly by differences in growth rate between study areas ($p > 0.05$, ANOVA) as found by SEED (*op. cit.*).

Significant differences were found in the shell weight to tissue weight ratios between the study sites (Table 2). Crisfield mussels have proportionately more shell weight than those of either of the other sites ($p < 0.05$, ANOVA), and Cape Charles mussels have more shell weight than Tom's Cove *Geukensia demissa* ($p < 0.05$, ANOVA). Since calcium availability may be low in low salinity waters, the opposite relationship might have been expected between the study areas (LOWENSTAM, 1954; GRAUS, 1974). The results on growth rates (Figure 4) shed light on this apparent contradiction. The slow-growing mussels from Crisfield have the heaviest shells while the rapidly growing

Table 2

Shell shape and body size relationships of *Geukensia demissa* found at the study sites
(Tom's Cove = 210, Cape Charles N = 111, Crisfield N = 130). Significance was determined by ANOVA.

Parameters	Study site	Regression equation	Significance
Length *vs* Height	Tom's Cove	$Y = 2.75 + 0.38X$	$p < 0.001$
(X)　　　(Y)	Cape Charles	$Y = 2.37 + 0.38X$	$p < 0.001$
	Crisfield	$Y = 1.25 + 0.40X$	$p < 0.001$
Length *vs* Width	Tom's Cove	$Y = -0.77 + 0.32X$	$p < 0.001$
	Cape Charles	$Y = -0.52 + 0.32X$	$p < 0.001$
	Crisfield	$Y = -3.00 + 0.32X$	$p < 0.001$
Length *vs* Height/Width	Tom's Cove	$Y = 1.6 - 0.003X$	$p < 0.05$
	Cape Charles	$Y = 1.6 - 0.003X$	$p < 0.05$
	Crisfield	$Y = 1.6 - 0.004X$	$p > 0.05$
Shell *vs* Tissue	Tom's Cove	$Y = 0.01 + 0.08X$	$p < 0.001$
Weight　Weight	Cape Charles	$Y = 0.09 + 0.06X$	$p < 0.001$
	Crisfield	$Y = 0.06 + 0.04X$	$p < 0.001$